Linking Habitat-related and Density-dependent Population Responses in Chinook Salmon

Correigh M. Greene *and* ***Timothy J. Beechie***
Division of Environmental Conservation, NOAA Fisheries, Northwest Fisheries Science Center

Eric Beamer
Skagit System Cooperative

Abstract
Efforts to improve the viability of salmon populations depend on understanding the consequences of habitat change, but our ability to predict these consequences is often hampered by a poor understanding of habitat relationships and their effects on population dynamics. We constructed a watershed-scale Leslie matrix model of chinook salmon that specified residency in redds, streams, tidal deltas, nearshore habitats, and the ocean. Using this model, we compared the relative importance of different habitats under several different density dependent scenarios: density independence throughout the life cycle, density independent survival with a spawning capacity (a "hockey stick" model), density-dependent survival in the streams and tidal delta, and density-dependent movement among streams, delta, and nearshore. All scenarios indicated that population dynamics were most sensitive to changes in nearshore and ocean mortality. However, sensitivity to changes in freshwater and delta productivity and capacity varied among the different density-dependent scenarios. These findings indicate that (1) nearshore habitat relationships may play particularly significant roles for salmon population dynamics, and (2) the relative importance of stream and tidal delta habitats will largely depend upon the form of density dependence influencing salmon stocks.

Introduction
Habitat degradation and loss have been listed as major causes of population declines in Pacific salmon (*Oncorhynchus* spp.) (Nehlson et al. 1991). However, evaluation of the extent to which freshwater habitat degradation has reduced survival rates, relative to changes in marine survival and harvest, is complicated by the fact that anadromous salmonids use a number of different aquatic habitats during their life cycle including streams, estuaries, bay or nearshore environments, and marine habitats. In order to assess the merits of management actions (e.g., habitat restoration) that might improve population size, we need to evaluate the contribution of different aquatic habitats to density-dependent population dynamics. We can do this theoretically using life cycle models (Greene and Beechie submitted) and we can also do this empirically (Greene et al. submitted) to validate the theory. The combination of approaches allows us to make some important generalizations about habitat-relationships and their population consequences.

Our modeling efforts for ocean-type chinook salmon (*O. tshawytscha*) are based on disaggregating the life cycle into discrete stages. Juveniles start as eggs in redds, where they incubate for approximately five months before emerging. They then spend up to three months rearing and migrating downstream before entering the tidal delta, where they can spend up to two months rearing. Thereafter, juveniles migrate to nearshore environments such as bays, inlets, and pocket estuaries, rapidly growing until the end of the first year, when they begin their migration north in the ocean (Healey 1991). Residency in the ocean is generally three to five years, and then adults migrate back through these habitats to spawn.

This view disaggregates the life cycle into stages that many researchers have considered the important transitions for chinook salmon populations. Disaggregating the life cycle allows us to consider different habitat conditions affecting salmon during residency in these different habitats, as well as the effects humans have on salmon populations.

We want to ask—where should we focus our efforts? Which actions would result in the biggest response by salmon populations?

The potential for restoration can be pretty large. Collins et al. (2003) showed that habitat loss in the Skagit River tidal delta was greater than 80% over the period between 1850 and 1950. This loss was largely due to diking for agriculture and residential areas. Habitat loss (as opposed to degradation of existing habitat) has the potential to limit population growth due to reductions in the system's carrying capacity. If this were the case, density dependent population limitations occurring at particular life stages would limit population size, even if the population were at low density due to other factors influencing the population.

In the Skagit River, we do see evidence of density dependence. Long-term monitoring of habitat use at eight sites in the Skagit River delta has revealed that the density of chinook salmon increases as a function of outmigrant population size at low outmigrations, but levels off at high outmigration sizes.

A Beverton-Holt relationship can explain about 30% of the variation in density among sites as a function of outmigrant population size (Beamer et al. in prep.). This type of density dependence is often interpreted as density-dependent survival, whereby the leveling off occurs as a result of mortality. However, in migratory fish other explanations are possible.

In the Skagit System, several life history types exist, including fish that rear for an extended period in delta and fry migrants, fish that quickly pass through delta and migrate straight into the nearshore habitats of Skagit Bay. The proportion of fish during the early migration that are fry migrants increases as a function of the outmigration size (Beamer and Rice in prep.).

This suggests an alternative to density dependent survival that we call density dependent movement. A simple way to think about it is that as the delta fills up, smaller fish are forced through the system into the nearshore.
So, in the salmon life cycle, we have different habitats and also different possible scenarios for density dependence. Both of these factors may influence the efficacy of restoration efforts. We wanted to ask 1) how important are particular aquatic habitats to Chinook salmon population persistence and 2) how do three possible density dependent mechanisms affect the importance of aquatic habitats? To answer them, we integrated habitats into a life cycle model and examined three hypothetical scenarios: (1) density independence in juvenile habitats; (2) density-dependent survival in stream and delta habitats; and (3) density-dependent movement among stream, delta, and nearshore habitats. We also validated these results using a statistical analysis of factors occurring at different life stages that influenced return rates of chinook salmon to the Skagit River.

Methods

Life Cycle Model. The basic construct for the models follows our conceptual view of the life cycle (Greene and Beechie submitted).

The simplest scenario is the density independent survival scenario. In this scenario we simply specify habitat-specific survival parameters that represent transition rates among different habitats (Figure 1). These parameters are based on the best available estimates for the Puget Sound region. Density-dependent parameters are based on a hypothetical watershed characterized by stream, delta and nearshore habitats of different areas.

We assume the existence of a spawning capacity limiting the number of spawners, based on stream area. In the two density-dependent scenarios, we assume that a Beverton-Holt function controls recruitment from one habitat to the next. In the density-dependent survival scenario, we assume the flattening out of the recruitment curve represents mortality above capacity, while in the density dependent movement scenario, we assume it represents downstream movement of fish entering the habitat when it is above capacity. Capacity is determined by two additional parameters, stream and delta area.

We test the sensitivity of each habitat parameter to change by first calculating the productivity of the baseline situation at present, and then perturbing the population using a 5% change in each parameter shown in Fig. 1. The sensitivity, then, is defined as the percentage change in escapement resulting from the perturbation.

Statistical Model. A true validation of the life cycle model would involve habitat restoration in different habitats, a hugely complicated undertaking. However, we can get some sense of the validity of the results by correlating return rates of salmon with natural changes within these habitats. To do this, we used a regression model that related Skagit River recruits per spawner of 1974-90 brood years with environmental conditions experienced during residency in four different habitat types (Greene et al. submitted). The assumption is that these conditions correlate with survival during residency within these habitats. So, we related return rate with flood recurrence interval during egg incubation and freshwater residency; sea surface temperature (SST), sea level pressure (SLP), sea level, and upwelling (UPW) during delta and nearshore residency; and SST, SLP, and UPW during three ocean years. For these marine-influenced systems, we incorporated multiple variables in a principal components analysis and used the first principal component (referred to hereafter as the habitat factor) as the main predictor for that habitat. Density dependence was tested for by including the estimated number of eggs in each brood year.

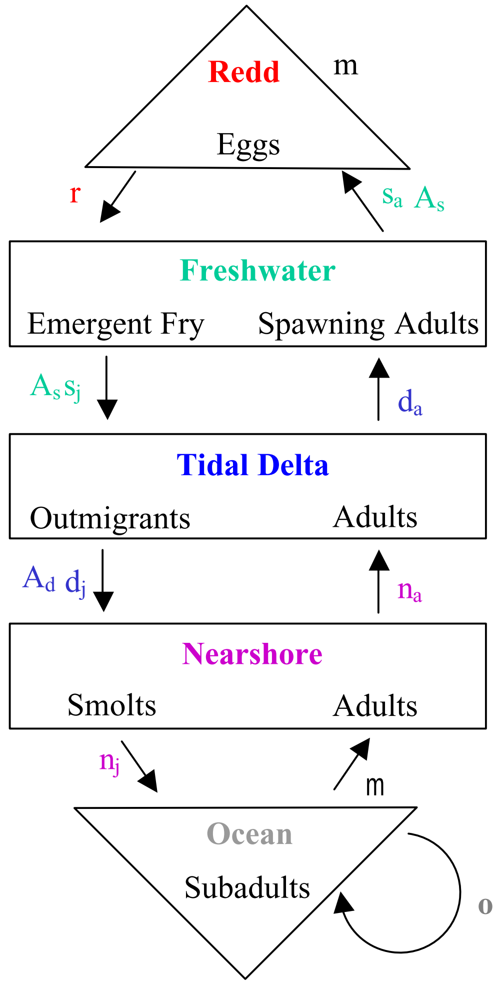

Figure 1. Schematic for the life history model. As fish migrate through each habitat (redd, stream, tidal delta, nearshore, and ocean), they incur mortality based on survival parameters (r = redd survival, s = stream survival, d = delta survival, n = nearshore survival, o = ocean survival, μ = survival through harvest, subscripts denote parameters for either juveniles (j) or adults (a), and fecundity (m). For density-dependent scenarios, the population dynamics are also influenced by habitat area (A_s = stream area, A_d = delta area).

Results

Life Cycle Model. The results of the life cycle model revealed that restoration potential for the most important habitat parameters depends upon the three density dependent scenarios (Figure 2). In Figure 2, any score above a 5% increase in escapement represents a proportionally greater return in escapement for the management "investment."
Several patterns emerge from these results. First, in all scenarios, escapement is most sensitive to changes in nearshore and ocean survival. Second, the sensitivity of escapement to changes in stream and delta parameters depends upon the mechanism of density dependence. In all three scenarios, a 5% improvement in stream, nearshore, and ocean survival results in more than a 5% change in escapement. Only in the density-dependent survival scenario do changes in tidal delta parameters have a similar effect. Note that if we assume that these results are additive, we could combine the results for both redd and stream habitats to represent the percentage increase in escapement resulting from an improvement in **freshwater** survival. These results suggest that this change might have quite a strong effect, in some cases even higher than the sensitivity of ocean survival.

Statistical Model. The statistical model confirmed the main results of the life cycle model. The best model based on an AIC analysis (Akaike's Information Criterion, Burnham and Anderson 2002) predicted a surprising 90% of the variation in recruits per spawner. The best model included eggs, flood recurrence interval, and the principal components factors describing environmental conditions during nearshore and three ocean years of residency. Environmental conditions

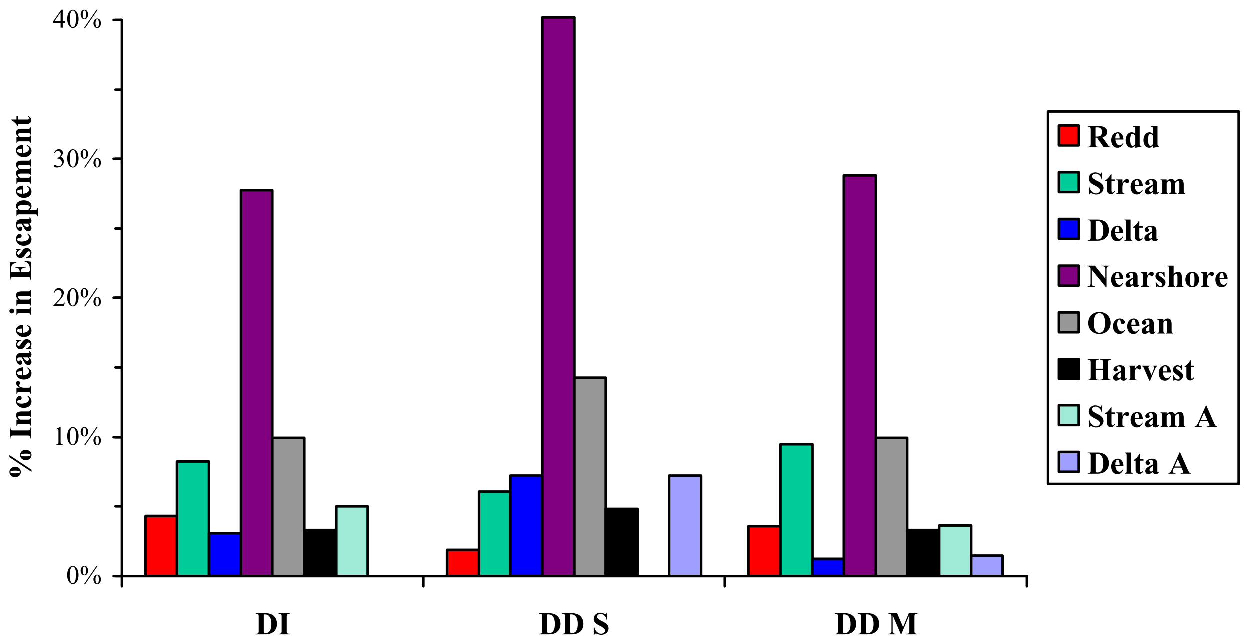

Figure 2. Sensitivity of spawner abundance to a 5% change in mortality or area associated with different habitats, for three possible scenarios: density independence (DI), density-dependent survival (DD S), or density-dependent movement (DD M) in stream and delta habitats. Solid-colored bars indicate sensitivity of survival parameters, while hatched bars represent sensitivity of habitat area parameters.

experienced during delta residency were not in the best model. Three particularly important results emerge upon inspection of the relationships of each of the variables with return rate. First, there is density dependence, based on the negative correlation of return rate and eggs. Second, the two most important predictors of return rate are flood recurrence interval and the nearshore PCA factor. Together with eggs, these variables explain 74% of the variation in return rate. Third, environmental conditions experienced during ocean residency explain only an extra 16% of the variation. Interestingly, the relationship between return rate and ocean factor is not constant across ocean years, going from negative in the first ocean year to positive in the third ocean year.

Conclusions

The results of the life cycle model and the statistical model revealed some striking parallels.

The life cycle model suggests that population abundance is generally most sensitive to changes in survival occurring in the nearshore and freshwater life stages (in that order), but that the population's sensitivity to changes in survival and habitat area depend upon the presumed mechanism of density dependence. Meanwhile, the results of the statistical model reveal that environmental conditions experienced during freshwater and nearshore residency are the most important predictors of return rate, and that fish experience strong density dependence. However, in contrast to the predictions from the model, the statistical analysis suggests that conditions experienced during ocean residency are less important than other conditions and fairly variable.

Some caution of directly linking the two analyses is in order. Just because a life stage is sensitive to environmental variation does not necessarily mean that it will be responsive to restoration, either because there is little restoration possible or because the processes influencing survival in a particular habitat are out of our control. For example, we know of few "fixes" to changes in ocean conditions, so the extent to which salmon populations are sensitive to changes in ocean conditions is largely a constraint on our ability to mitigate population declines. We might similarly ask this question about nearshore conditions, the habitat predicted by our model to be most sensitive to changes in survival, and thus implying large restoration benefits restoration. We know little about the habitats salmon use during nearshore residency and the degree to which we have modified them. However, we do know that this life stage is associated with high mortality (Healey 1980, Bravender et al. 1999) and changes in body size (Levings 1994, Korman et al. 1997). If current nearshore conditions are significantly affected by human activities such as sea grass removal, bulkheading and dredging, salmon populations may be quite sensitive to their restoration, especially if such restoration can ameliorate the strong negative effects of environmental variation that we detected in our statistical analysis. These theoretical results point to the need to answer basic questions about salmon habitat use and ecology in nearshore habitats, which can be done only through field-based studies.

A better understanding of the basic biology is also needed to understand the importance of delta and stream habitats as well. In particular, the life cycle model results demonstrates that it really matters to know the mechanisms of density dependence acting on the stock of chinook salmon that managers want to restore, lest we focus on the wrong recovery actions. In the Skagit system, our statistical analysis confirms the existence of strong density dependence, and independent analyses of habitat use measured in the field (Beamer et al. in prep., Beamer and Rice, in prep.) indicate that much of this density dependence occurs within the tidal delta. However, the mechanisms accounting for this density dependence are still unanswered. Several nonexclusive possibilities include density-dependent survival or growth within the delta, and density-dependent movement from the delta into the nearshore.

What is clear is that fish do rear in restored tidal delta habitats in the Skagit River (Beamer and LaRock 1998) and elsewhere (Shreffler et al. 1990) in large numbers. In both natural and restored delta environments, tidal channels represent highly productive and protected areas for chinook salmon. Indeed, the fact that our statistical analysis revealed no correlation of return rate with environmental conditions experienced during delta residency may indicate not that the delta is unimportant, but that it is an extremely important population "buffer". In other words the delta may be a relatively stable zone within a series of habitats characterized by large environmental variation. If this is the case, we should not be surprised that the remnant delta habitat would be highly preferred by salmon, and therefore the site of intense density dependence. As indicated by the life history model, the response of the population to ongoing restoration in the delta will depend not only on a better understanding of density-dependent interactions within the delta, but also on what is occurring in both upstream and downstream habitats. Therefore, local managers considering which restoration actions to advocate need field confirmation of the relevant biological mechanisms to inform that population models that provide us answers concerning recovery options.

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